



# Biogeographic provinces in the Atlantic deep sea determined from cumacean distribution patterns

Les Watling

Department of Zoology, University of Hawaii at Manoa, Honolulu, HI 96822, United States

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## ABSTRACT

Cumacean species abundance and presence–absence data were compiled from samples taken along the US northeast slope and rise, from around the Faroe Islands, and from deep-sea transects throughout the Atlantic Ocean. These data were analyzed using hierarchical cluster techniques, the results being used to help determine the boundaries of zoogeographic units in the deep sea. Comparing the results of these analyses with previous studies on protobranchs, tunicates, and sea stars, supports dividing the deep Atlantic Ocean into the following biogeographic units: (1) Norwegian Basin; (2) North Atlantic Upper Bathyal; (3) West European Basin Northern Bathyal; (4) Lusitanian Bathyal; (5) North American Basin Bathyal; (6) West European Basin Abyssal; (7) North American Basin Abyssal; and (8) Angola, Cape, Brazil, and Argentine Basins occupying the more or less isolated basins of the South Atlantic Ocean. These latter are not well-sampled for most groups but appear to be separated from each other.

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## 1. Introduction

Despite the fact that the North Atlantic Ocean is probably the best-sampled of all deep-sea environments, there is yet no comprehensive biogeographic analysis of the resident species. Patterns of diversity are well-explored (e.g., Rex et al., 2000; Lamshead et al., 2000) as are community structure (e.g., Grassle and Maciolek, 1992) and ecological relationships (e.g., Flach and Heip, 1996, among others). Biogeographic patterns have been investigated for a few deep-sea taxa, e.g., protobranchs (Allen and Sanders, 1996), asteroids (Sibuet, 1979; Price et al., 1999), and tunicates (Monniot, 1979) living in the deep basins, and octocorals (Watling and Auster, 2005), scleractinians (Cairns and Chapman, 2001), hydroids (Henry et al., 2008), and fish on the continental slopes (Haedrich and Merrett, 1990; Koslow, 1993). Recently, the biogeographical relationships of several invertebrate taxa found on the Reykjanes Ridge and Northeastern Atlantic seamounts were summarized by Mironov et al. (2006) and Mortensen et al. (2008). Vinogradova (1979) produced a biogeographic map of abyssal and hadal fauna for the world ocean, but did not offer many details of the macrofauna on which her map was based.

Cumaceans are a useful group for biogeographic analyses because they have very limited dispersal capabilities. They live at the sediment–water interface, usually partially buried in the sediment in order to feed and escape the notice of predators. Young ones are carried by the female in a ventral brood pouch and hatch nearly fully formed and capable of caring for themselves.

Only the adult males of some cumacean families have elaborate swimming appendages on the abdomen, but most have some paddling capabilities associated with their thoracic legs. Nevertheless, most cumaceans are not good swimmers, and these deep-sea dwellers are not likely to rise far off the bottom when moving around. Thus, patterns observed for cumaceans should be useful for other benthic invertebrate groups with limited dispersal capability, but these patterns also may be more spatially restricted than what might be observed for taxa with long-lived larvae.

Cumacean data for the North Atlantic come from several major sampling programs. The earliest (1960s) was a series of deep-sea transects organized by Howard Sanders and conducted under the auspices of the Woods Hole Oceanographic Institution. Sampling was by means of an epibenthic sled that skimmed along the sediment–water interface. Other transects were sampled using similar gear by what is now IFREMER (Institut Français pour l'Exploration de la Mer) and the Scottish Association for Marine Science (SAMS). Details of those sampling programs and an analysis of broad-scale trends in diversity are given by Gage et al. (2004). During the mid-1980s a total of 424 quantitative box-core samples were taken between Cape Hatteras and the northern end of Georges Bank (approximately 37–41°N) at depths ranging from 1500 to 2500 m in the southern sampling area and from 250 to nearly 2200 m in the north. Details of this sampling program are available only in unpublished reports (Maciolek et al., 1987a, b), and the cumacean data have not been further analyzed. The only other comprehensive sampling program comprises a series of quantitative and qualitative samples taken first around the Faroe Islands (BIOFAR) in the early 1990s followed by a similar effort

E-mail address: [watling@hawaii.edu](mailto:watling@hawaii.edu)

around Iceland (BIOICE) in the late 1990s. Data on the BIOFAR sampling program are available in [Nørrevang et al. \(1994\)](#) and the cumacean data were summarized by [Gerken and Watling \(1999\)](#) and [Watling and Gerken \(2005\)](#).

[Jones and Sanders \(1972\)](#) gave the first overview of cumacean distributions using the samples from the Woods Hole transects. Data from four transects were analyzed: (1) from Gay Head, Massachusetts in the eastern US, to Bermuda; (2) from the Bay of Biscay in the NE Atlantic; (3) from off the Canary Islands in the NE Atlantic; and (4) from the transect between Dakar in western Africa and Recife on the northeastern corner of Brazil. In general, more than half the species from the South Atlantic (as represented by the Dakar–Recife transect) were not found in the North Atlantic, and there was a strong separation of species in the western and the eastern basins of the North Atlantic. [Reyss \(1973\)](#) compared samples from the Mediterranean to those from the North Atlantic and found that 19 of 33 Mediterranean species identified were previously known, primarily from the nearby Bay of Biscay. Surprisingly, however, 13 of the 19 species were also known from the Gay Head–Bermuda samples. On the basis of additional samples immediately inside and outside the Straits of Gibraltar, [Jones \(1990\)](#) concluded that the Mediterranean cumacean fauna consisted of a subset of the Atlantic species with a few Mediterranean endemics also present. [Watling and Gerken \(2005\)](#) identified the cumaceans from the BIOFAR samples and related their distribution around the Faroe Islands to the prevalent water masses. They noted that at shelf and shallow slope depths, there was little correspondence of the cumacean fauna to that of the NW Atlantic. In addition, the deep fauna to the north of the Faroes–Iceland Ridge seemed to be mostly confined to the Norwegian Sea water colder than 1 °C.

In this paper, the broad distributional patterns of cumaceans found primarily at sampling sites deeper than 300 m will be examined with a view to delimit deep Atlantic zoogeographic provinces. While there are still significant gaps in the data set as compiled, some understanding of cumacean distributions can be developed for the data available.

## 2. Methods and materials

The cumacean data used in this paper were compiled from three sources: my own unpublished data from the US North Atlantic Continental slope and rise ([Maciolek et al., 1987a, b](#)) along the US east coast north of Cape Hatteras, [Watling and Gerken \(2005\)](#) compilation of data from BIOFAR samples in the vicinity of the Faroe Islands, and cumacean data for the Atlantic Basins compiled by late Norman Jones and summarized by [Gage et al. \(2004\)](#), most graciously contributed in spreadsheet form by John Bishop.

A multitude of sampling devices, ranging from epibenthic sleds to box corers, were used to obtain the samples from which these data are derived, so all analyses were done using 4th root transformed abundance data or by transforming to presence–absence. Biogeographic pattern analysis can utilize a variety of methods, but most often involves either hierarchical cluster analysis or multidimensional scaling of data from discrete samples or from aggregations of records from a variety of sources grouped by “location” (see for example, [Rosen, 1988](#)).

In this study, assemblages of species were determined using the hierarchical cluster analysis routine CLUSTER in the program PRIMER 6 ([Clarke and Gorley, 2006](#)) based on the Bray–Curtis similarity measure for abundance data or Sorensen’s coefficient for presence/absence data. When using CLUSTER, the permutation test SIMPROF (at 1% level) was used to determine which clusters have significant internal structure. The latter are joined by light

dotted lines in the figures. Since most results were essentially similar, only the cluster-analysis dendrograms based on the Sorensen presence/absence measure will be presented. Important species for each cluster were determined using the routine SIMPER. Some stations from all data sets were not included in the final analysis because they were represented by only one or two species. In the end, the distributions of 210 species from 242 stations were used. The cluster results were plotted on a map of the Atlantic Ocean using the program ArcGIS 9.3.

The North Atlantic slope and rise samples cover a range of depths from 200 to 2500 m, with the shallowest stations occurring along the northeastern edge of Georges Bank ([Fig. 1](#)). The stations are divided into 2 groups, designated NOR and MID, with the NOR stations ranging from 41.1°N, 66.2°W, to 39.7°N, 70.9°W, and the MID stations ranging from 39.1°N, 72.1°W to 37.9°N, 73.8°W. The 28 stations of the US North Atlantic slope and rise study produced 54 species in 15 genera. These stations were sampled 6 times over 18 months. The abundances of each species, and consequently the presence/absence of each species, were summed for each station over the 6 sample sets.

The Atlantic Basin data compiled by Norman Jones included 173 species in 38 genera taken at 129 stations sampled over a period of several years. These samples include several species from off the US east coast and extending out into the North American Basin, many from the Northeast Atlantic, primarily along the European and NW African slope and rise, and scattered samples from the slope and rise of the Guinea, Guyana, Angola, Cape, Brazil, and Argentine Basins. Depths of these samples range from 500 to 4800 m.

The BIOFAR samples included 68 species in 19 genera from 146 stations sampled over three years. A complete analysis of the BIOFAR data is given by [Watling and Gerken \(2005\)](#), but the data are included here because the samples are from a range of water-mass types. Some water masses, such as that referred to as Atlantic Water ([Hansen and Østerhus, 2000](#)) eventually become North Atlantic Deep Water as it flows southward and if the cumacean fauna is keyed to water masses as suggested by [Watling and Gerken \(2005\)](#), then there should at least be some overlap between some of the BIOFAR samples and those from the North Atlantic.

## 3. Results

Cluster analysis of all 242 stations produced two main clusters ([Fig. 2](#)), one for the shallow and slope samples from the BIOFAR and US east coast areas, and one for the samples from the Northeast Atlantic slope and all deep basins throughout the Atlantic. The first cluster is divided, on the basis of the SIMPROF analysis, into 2 main groups: [Fig. 2A](#), the US east coast slope and rise samples, and [Fig. 2B](#), samples primarily from the BIOFAR area. SIMPROF analysis divided the latter into several groups that are mainly characterized by their water-mass characteristics, as noted earlier by [Watling and Gerken \(2005\)](#).

The second main cluster is a bit more heterogeneous than the first, and can be divided into 6 groups using SIMPROF output. The first, [Fig. 2C](#), consists of 7 distinct clusters, each predominantly representing basins in the Northwestern and South Atlantic (e.g., Brazil, Guyana, Angola, and Cape Basins) at depths from 500 to 4400 m, with samples at similar depths clustering together. Cluster group D ([Fig. 2](#)) consists of 3 stations at depths from 3800 to 4700 m in the North American Basin. The remaining North American Basin stations are grouped together in cluster group G. Cluster groups E, F, H, and K include all the stations from the slope and rise from the Canary and Northeast Atlantic (West European) Basins. Cluster group E includes those stations in the Canary Basin

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